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DAILY METABOLIZED ENERGY CONSUMPTION OF OYSTERCATCHERS *HAEMATOPUS OSTRALEGUS* FEEDING ON LARVAE OF THE CRANE FLY *TIPULA PALUDOSA*

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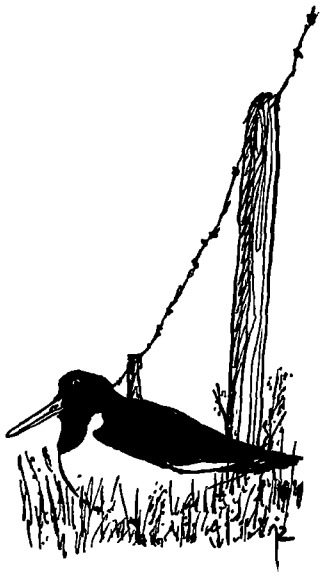

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Oystercatchers feeding on grassland in spring mainly take leatherjackets, the larvae of the crane fly *Tipula paludosa*. The birds roost at night and feed for 40 to 60% of the daylight period. Their intake rate during feeding is 1 to 1.5 mg AFDW or 20 to 30 J s^{-1}, which is rather low compared to the intake rates achieved on tidal flats. The digestibility of leatherjackets was estimated in three ways: ash and chlorophyll were used as natural digestibility markers, and prey remnants in the faeces were counted. On average, 86% of the ingested energy was assimilated. The daily metabolizable energy consumption was estimated to be 640 kJ, which is equivalent to 2.6 × *BMR*. The costs of living were relatively low because the birds lived in thermoneutral conditions and flew for only about 15 min a day.

Key words: Oystercatcher - *Haematopus ostralegus* - leatherjacket - *Tipula paludosa* - digestibility - daily energy intake

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INTRODUCTION

The first quantitative studies on the food consumption of Oystercatchers *Haematopus ostralegus* took place in the fifties and expressed the food intake in terms of wet weight or volume (e.g. Drinnan 1957, 1958). In later studies, the flesh of the prey was dried, and the inorganic fraction determined, in order to express the food intake in terms of dry flesh, or ash-free dry weight (AFDW). This was an important improvement since water and ash contain no energy, whereas the contributions of these fractions to the wet and dry weight, respectively is highly variable. Two further measurements are necessary, however, to determine the food intake in terms of metabolizable, or net, energy. The energy density of the food ought to be measured, as well as its digestibility, i.e. the fraction of the consumed energy that is actually assimilated. The energy density of the prey taken by Oystercatcher varies between 21 and 24 kJ g^{-1} dry flesh, but has been measured in only a minority of the many studies on the intake rate of Oystercatchers (Zwarts *et al.* 1996a & b). Digestibility has been determined for only one prey, the Mussel *Mytilus edulis*. Speakman (1987) found that 82% of the ash-free dry weight was absorbed. He did not measure the energy content of food and faeces, but if we use the values obtained in later studies (Zwarts & Blomert 1990, Kersten & Visser 1996), the digestibility must have been about 86-87%, which is close to the 85% actually found by Kersten & Visser (1996). It has still to be shown how well other prey are digested, although the digestibility is unlikely to deviate much from these values, as long as pure flesh is taken (Castro *et al.* 1989, Zwarts & Blomert 1990).

This paper describes field measurements on food consumption of Oystercatchers feeding in grassland. The large majority of the prey were

leatherjackets, larvae of the crane fly *Tipula paludosa*, usually supplemented with some earthworms. Since the energy content and the digestibility of the prey were measured, the metabolizable energy intake rate could be determined. Fortunately, the birds foraged in non-tidal habitat and spent the night on the roost. Hence it was also possible to estimate the daily metabolizable energy consumption by measuring the net intake rate during the daylight hours.

METHODS

The birds were studied in inland areas in the northern part of the Netherlands during three occasions. First, two pairs of Oystercatchers were observed in the province of Friesland on 10-14 April 1995. The birds occupied territories, but the ♀♀ had not yet started to lay eggs. Second, data were collected on a pair of breeding birds on 19 May 1991, also in the province of Friesland. Third, a flock of 30 non-breeding birds were watched on the Frisian island of Texel on 29 and 30 May 1991. In contrast to both Friesland areas, where the soil consisted of clay, the Texel area was sandy. In all three cases, the birds could be watched extremely well, since they fed on close-cropped, mowed grassland or in a field with very short grass, at a distance of 10 to 50 m from the car from which they were observed with a telescope (20-60 × 70). Hence, we could distinguish the prey taken, predominantly leatherjackets and occasionally worms, and could also see when faeces were produced. The variation in weight of the leatherjackets was not large, so we did not try to distinguish size classes with this prey, but the worms selected by the birds were referred to as 'small', 'middle' and 'large'. After the observations had been ended, we collected about eight recently produced faeces and took 12 soil cores (surface area 225 cm^2; depth 10 cm). The faeces were immediately stored in a freezer, while the worms and leatherjackets were extracted from the soil samples by carefully breaking up the turf. We divided the individual worms into three size categories in the same way as we had done shortly before in the field, after which also the worms and leatherjackets were stored in a freezer.

To be able to reconstruct the prey weight of the leatherjackets taken by the Oystercatchers, we measured the length of head capsules and the mandibles in the prey collected from the soil and those found in the faeces. We dried the individual faeces and prey for 3 days at 60°C. The ash content of the leatherjackets, earthworms and faeces were determined by burning a sub-sample for 2 h at 550°C. The energy content was measured with a calibrated Parr adiabatic calorimeter. The chlorophyll concentration was derived from the optical density in a spectrophotometer after 1 g dry matter was extracted with 100 ml 85% acetone (Kemmink & Dijkstra 1968).

The digestibility of the food was estimated in three ways.

(1) We used the indigestible ash content as a natural digestibility marker. The higher the ash % in the faeces (ash_{out}) relative to that in the food (ash_{in}), the higher the digestibility of the organic matter (Q_{afdw}):

$$Q_{afdw} = 100 - ((100 - ash_{out})/(100 - ash_{in}) \times ash_{in}/ash_{out}).$$

If the energy content of the ash-free fraction of the food (kJ_{in}) and the faeces (kJ_{out}) is entered into the equation, the digestibility in terms of energy (Q_{kJ}) is:

$$Q_{kJ} = 100 - ((100 - Q_{afdw}) \times kJ_{out}/kJ_{in}).$$

(2) Leatherjackets eat grass, and hence birds eating leatherjackets also ingest grass. This offers the opportunity to use an indigestible grass constituent as a natural digestibility marker. We selected chlorophyll as the marker because Endendijk-Woutersen (1976) concluded from her experiments with geese that this is a better non-digestible marker than crude fiber.

Chlorophyll and ash are only reliable markers if the faeces are not contaminated with substrate or grass. Hence we selected faeces that were easy

to collect and took much care to collect the faeces as cleanly as possible. Later on, while we searched for prey remnants using a binocular microscope, each accidentally collected bit of grass was removed. To be sure that we collected the prey with the same amount of chlorophyll or ash as those ingested by the birds, the prey were individually stored in small containers, immediately after they had been collected from the turf, in order not to loose excreted matter.

(3) The remnants of the leatherjackets in the faeces were used to calculate per prey the excreted organic matter and energy per leatherjacket. Since both these quantities were also known for the prey that were taken, a third method to estimate the digestibility was available as Oystercatchers did not regurgitate pellets. The number of leatherjackets in the faeces could be determined exactly. Although the head capsules were often fragmented, the jaws appeared to be very strong because we only found completely intact ones in the faeces.

RESULTS

Time budget

The behaviour of the two pairs in mid-April was registered during 23 h spread out over four days. Table 1 gives the details about their feeding behaviour. The breeding pair in mid-May and the non-breeding birds at the end of May were watched for only 4.5 and 1 h, respectively. Despite the limited period of observation, these data are also shown in Table 1 to allow comparison with the mid-April data.

Table 1. Time budget of Oystercatchers: % of time spent feeding and flying. The birds were inactive, and sometimes aggresive, during the remaining time, except for the birds observed in mid-May which devoted half of the time to reproductive activities. The last column gives total time per day spent on their feeding area and/or territory.

period	feed, %	fly, %	time, h
mid-April	57.3	1.7	14.7
mid-May	39.9	0.0	-
end-May	c. 40.0	0.0	17.3

The birds in mid-April arrived in the territory at 6.33 h, 22 min before civil twilight, and left 883 min later, at 21.16 h, this being 48 min after civil twilight. Between times, they foraged for 57.3% of the time and flew during 1.47%, or 12 min. Their nocturnal roost was only 2.5 km away, a distance which was covered in 3 min. Since the birds presumably did not fly at night, the total time spent flying can be estimated as 18 min a day.

The breeding pair in mid-May was observed in the middle of the day and what they did at night was unknown. Table 1 pooled the data for both birds. The ♀ foraged for 46% of the time and engaged in breeding activities for the remaining time. The ♂ foraged for 40% of the time, spent 14% in resting and aggression and engaged in breeding activities for 46%. Both birds did not fly during the short observation period.

The non-breeding birds watched at the end of May were present in the field from 5 to 22 h. The feeding activity of the flock was not quantified exactly, but estimated to be about 40%.

Prey choice and prey weight

Direct observations showed that the Oystercatchers only took two prey species, of which 80-95% were leatherjackets and the rest earthworms, even though earthworms were twice as common as leatherjackets in the turf of two of the three study sites (Table 2).

Body weight of the leatherjackets was regressed against the size of the head capsule and against the size of the mandible, separately for the animals collected during the three observation periods. Since all details will be published elsewhere, we will only give the main conclusions. Comparison of the size of the head capsules and jaws of leatherjackets found in faeces with those in the population on offer shows that the Oystercatchers took either the average prey size or prey that were slightly larger than average. The huge

Table 2. Prey selection (% leatherjackets in diet) and prey density (density of leatherjackets and earthworms m^{-2}).

period	Lj, %	Lj m^{-2}	worm m^{-2}
mid-April	96	45	96
mid-May	86	78	135
end-May	84	148	102

difference in prey weight between mid-April and May (Table 3) was, therefore, completely due to growth of the prey. The observed growth fitted within the annual life cycle of the species concerned, the crane fly *Tipula paludosa*. The flies emerge in late summer, after which the ♀♀ lay, within a few days, their eggs, which hatch after a fortnight. Larvae remain very small in autumn and winter (< 1 cm), but as soon as the soil warms up in spring, they grow very rapidly until the end of May, when they reach a length of 3 to 4 cm. After that, the body weight does not increase, or even decreases, until August, when they pupate (e.g. De Jonge 1925, Laughin 1967, Den Hollander 1975).

Leatherjackets contained less inorganic matter than earthworms (Table 3). Such a difference was to be expected since leatherjackets are selective herbivores while earthworms ingest substrate. The energy content of leatherjackets was higher than that of earthworms (Table 3), which was mainly due to a difference in the fat content which is twice as high in leatherjackets as in earthworms (Blomert & Zwarts unpubl.). The energy content of leatherjackets taken by the Oystercatchers was 23 to 24 kJ (Table 3). This is rather low compared to 24 other samples collected by us in the same areas and months in other years. On average, the energy content of leatherjackets slightly increased from 24 kJ in March to 25 kJ in May and decreased again to 24 kJ in June.

Intake rate and defecation

Oystercatchers took their prey at a much higher rate in mid-April than later in the season, but if the prey weight is taken into account, the trend was in the opposite direction (Table 4). The intake rate was rather low, however, being twice as low as the average intake rate that Oystercatchers attain on tidal flats. The difference was even larger if the comparison is restricted to the rates on tidal flats on the same time of the year, in spring (Zwarts *et al.* 1996a). The three estimates of the intake rates did not differ from other inland studies (Zwarts *et al.* 1996a). Thus, apparently, Oystercatchers are less successful foragers in grassland than on tidal flats.

Oystercatchers produce droppings at regular intervals. The average interval was 406 s (SD = 205; n = 47) in mid-April, but the breeding birds observed in mid-May produced while actively foraging a dropping every 633 s. Since the birds did not defecate during their intervening breeding bouts, the average dropping interval was 1472 s in total. The dry weight of the faeces differed between the three observation periods (Table 5). The faeces of the breeding birds were 8 times as

Table 3. Average dry weight of selected prey (mg), % inorganic matter (ash) and energy content (kJ g^{-1} AFDW) of leatherjackets and earthworms. Since the energy content of the worms in April was not determined, the long-term average is given.

	leatherjackets			earthworms		
period	mg	ash	kJ	mg	ash	kJ
mid-April	17	15.4	22.9	59	23.3	c. 22.3
mid-May	40	12.5	23.1	45	23.4	20.0
end-May	70	25.3	23.8	87	39.6	22.4

Table 4. Feeding rate (prey min^{-1}) and intake rate (mg AFDW s^{-1} and Watt (J s^{-1})) while feeding. Intake rate is the product of feeding rate and prey weight (Table 3).

period	prey min^{-1}	mg s^{-1}	Watt
mid-April	3.12	1.04	19.0
mid-May	2.49	1.45	32.9
end-May	1.47	1.28	30.2

heavy as in mid-April, thus they overcompensated for the 3.6 times longer dropping interval.

Beside the dropping intervals we also determined the number of leatherjackets per dropping (Table 5). It was possible to calculate the rate at which these prey were processed. In mid-April the processing rate was 1.86 leatherjackets per min and for mid-May it was 1.01 leatherjacket min^{-1}. This outcome can be compared to the rate at which leatherjackets were ingested, including the non-feeding periods; this could be done as the feeding activity (Table 1), the % prey that were leatherjackets (Table 2) and the feeding rate while feeding (Table 4) were all known. Combining this information, the feeding rate must have been 1.72 and 0.85 leatherjacket min^{-1} in mid-April and mid-May, respectively. This is equivalent to 92 and 84%, respectively, of the gut processing rate.

The storage capacity of the Oystercatcher is so large that the bird can continue to digest its food for many h after feeding has ended (Kersten & Visser 1996). That is why the feeding rate can be much higher than the processing rate, at least over a limited feeding period (Zwarts *et al.* 1996b). The birds studied by us spent, however, 13 to 17 h in their feeding area. Taken over such a long period, the intake rate calculated over the feeding and non-feeding intervals combined cannot be much above the processing rate. Indeed, it was found that the feeding and processing rates were about the same. In retrospect, we believe that the processing rate was slightly overestimated, however, because droppings were not collected at random. Instead, our selection of faeces was probably biassed towards the larger than average ones because smaller faeces were probably more often overlooked. Indeed, small ones may even have been rejected to avoid collecting the faeces of smaller bird species. If so, the processing rate was presumably just below the intake rate with non-feeding periods included.

Digestibility

The ash content in the faeces (Table 5) was about twice as high as in the food (Table 3). Using the equation given in Methods, the digestibility was estimated at 83-92% (Table 6). The alternative method of counting prey fragments in the faeces gave nearly the same result in two of the three cases, but it was only 63% in one case. Although it cannot any longer be checked, it seems likely that, in the latter cases, part of the jaws was overlooked because the time spent sorting out a unit weight of faeces was less than in the other two series. Chlorophyll could not be measured separately in leatherjackets taken by the Oystercatchers during the three observation periods, but if all leatherjackets were taken together per month and compared to faeces of Oystercatchers and other wader species produced in the same months, the digestibility came out at 85.7% in April, 79.4% in May and decreased further in the following months. These values were close to, but

Table 5. Dry weight (mg), % ash and energy content (kJ per g AFDW) of the faeces. Last two columns give the number of leatherjackets per dropping (Lj) and the average time interval between two droppings (s).

period	mg	ash, %	kJ g^{-1}	Lj, *n*	s
mid-April	103.7	62.2	19.0	12.62	406
mid-May	848.0	45.9	17.4	>24.83	1472
end-May	342.5	55.7	13.0	7.12	-

Table 6. Digestibility of leatherjackets (% energy) according to three methods, using ash or chlorphyll as marker, or by counting jaws and head capsules in the faeces.

period	ash	chlorophyll	jaws
mid-April	89	86	85
mid-May	86	79	>63
end-May	83	-	81

consistently 5% lower than the estimate derived from the ash content.

We think that the data on ash content give the most reliable estimate of the digestive efficiency. Jaws may be overlooked and thus tend to produce an underestimate of the digestibility, whereas chlorophyll could only be determined in pooled data.

Daily metabolized energy consumption

The estimation of the daily metabolizable energy consumption is based upon the product of 6 variables: the time spent on the feeding area (Table 1), the feeding activity (Table 1), the feeding rate (Table 4), the prey weight (Table 3), the energy content of the prey (Table 3) and the digestibility (Table 6). All six variables were quantified in mid-April. The net consumption was 640 kJ day^{-1}. For mid-May, the observation period was too short to arrive at an accurate estimate, but assuming that the birds continued to feed for the entire daylight period at a rate similar to that recorded in the observation period itself, the consumption would be 809 kJ. We know that the flock of non-breeding birds observed at the end of May spent the entire daylight period on the feeding area, but the feeding activity was not quantified exactly. But assuming that the estimate of 40% was correct, the consumption would be 626 kJ. Hence, although the latter two estimates of the net energy consumption are less reliable, they do not differ much from the 640 kJ calculated for mid-April.

DISCUSSION

Are leatherjackets preferred above earthworms?

Leatherjackets are taken much more frequently than earthworms, perhaps because Oystercatchers prefer their higher energy content and lower inorganic loading (Table 3). An alternative explanation is that birds searching for surfacing leatherjackets reach a higher intake rate than birds searching for earthworms. Certainly, if earthworms remain deeply buried beneath the surface, searching for leatherjackets is not compatible with searching for earthworms and this may explain the apparent overriding preference for leatherjackets. Leatherjackets are an easy prey for Oystercatchers because they live in U-shaped burrows that are usually 2 to 4 cm deep. In spring, it is not even necessary to extract the leatherjackets from their burrows, since they are then often found at, or just beneath, the surface. Earthworms also emerge at the surface but they usually remain for most of their time in their burrows that are 5 to 10 cm deep and are thus less easy to find. Moreover it takes birds more time to extract earthworms from the turf than leatherjackets. Hence, it is not surprising that Oystercatchers in spring and summer take more leatherjackets than earthworms. This is completely different from August to March, when Oystercatchers foraging in grassland only take earthworms. There are no leatherjackets in late summer and autumn, whereas they are too small in winter to be a profitable prey for Oystercatchers.

Maintenance metabolism

The body weight of Oystercatchers remain constant at 500-510 g in April-June during their presence on the inland breeding areas (Zwarts *et al.* 1996c). We do not know the individual body weights of the birds observed in April and May, but we assume that the average weight of the observed birds was also 510 g and did not change during the three observation periods. The estimated consumption of 640 kJ day^{-1} should therefore be enough to keep their body weight con-

stant. Indeed, this estimate closely fits with other estimates of the daily energy consumption in free-living and captive birds at constant body weight (Zwarts *et al.* 1996b: Fig. 3). It also closely agrees with four other estimates of the daily gross consumption of Oystercatcher feeding on grassland in April and May (Hosper 1978), but deviates much from the single estimate of March (Veenstra 1977; see also Zwarts *et al.* 1996a: study 55, 56, 242, 244, 249 in the appendix).

How to explain the low food consumption in March? Oystercatchers usually take earthworms shortly after arrival on the inland breeding areas, but Veenstra (1977) observed on 17 March a flock of birds feeding on leatherjackets in a meadow from sunrise to sunset. During these 13 h, the birds foraged for 59.1% of the time and took 1.37 leatherjackets min^{-1} feeding, on average, and thus in total 639 leatherjackets per day. He did not measure the weight of the prey, but if we assume it was 14 mg at a maximum, i.e. the prey weight some weeks later (Table 1), the daily consumption would be 9 g AFDW at a maximum (see Zwarts *et al.* 1996a: footnote at study 249 in appendix). Assuming that (1) this 9 g is correct and that, moreover, (2) the energy content of leatherjackets is 24 kJ and that (3) 89% of the prey energy is assimilated, the daily net consumption would be 194 kJ at the utmost, or 30% relative to the 640 estimated for mid-April.

Oystercatchers lose 100 g body weight after arrival on the inland breeding area by catabolizing 67 g fat and 6 g of their lean dry flesh weight (Zwarts *et al.* 1996c). This energy drain is equivalent to 2700 kJ. Assuming that 640 kJ day^{-1} is sufficient to keep their body weight constant, it takes 4.2 days to lose this amount of stored energy reserve. However, when their daily consumption is 194 kJ, the period of weight loss will be extended from 4.2 to 6 days. The weight loss is indeed confined to less than a fortnight (Zwarts *et al.* 1996c). It is unlikely that the weight loss in March is due to the poor feeding conditions or to the short feeding period caused by the limited daylight period. If this were the case, the birds would not rest for 40.9% of the available feeding time, whereas the intake rate during feeding and non-feeding time combined is still too low to be constrained by the digestive system (Kersten & Visser 1996). In other words, the daily consumption was low in March because the birds mobilized the nutrient reserve that they no longer needed in early spring.

The basal metabolic rate (*BMR*) of Oystercatchers amounts to 250 kJ (Kersten & Piersma 1987). The daily net consumption in April is thus $2.56 \times BMR$. This is below the modal value of $3 \times BMR$ found by Bryant & Tatner (1991) in their overview of the daily energy expenditure in small birds, but still within the usual range of 2-4 $\times$ *BMR*. A relatively low energy expenditure was to be expected for Oystercatchers in April and May, because the prevailing air temperatures are usually far above the lower critical temperature of 9°C (Kersten & Piersma 1987), so that there are no extra thermoregulation costs. Moreover, the birds hardly fly, feed during less than 30% of the day and are inactive during the majority of the time.

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SAMENVATTING

Scholeksters die in het voorjaar in grasland foerageerden aten vooral emelten, de larven van de langpootmug *Tipula paludosa*. De vogels brachten de nacht door op gemeenschappelijke slaapplaatsen en tijdens de daglichturen foerageerden ze 40 tot 60% van de tijd. Hun opnamesnelheid tijdens het voedsel zoeken was 1 tot 1.5 mg as-vrij droog vlees per seconde of 20 tot 30 Joule per seconde. Dit is tamelijk laag vergeleken met de opnamesnelheid die Scholeksters op het wad halen. De verteerbaarheid van emelten werden op drie manieren geschat: as en chlorophyll werden gebruikt als natuurlijke merker en prooirestanten in de faeces (kaken en koppen van emelten) werden geteld. Gemiddeld 86% van de opgenomen energie werd geassimileerd. De dagelijks gemetaboliseerde energie consumptie werd geschat op 640 kJ. Dit stond gelijk aan 2.6 maal het basaal metabolisme. Het levensonderhoud was niet erg duur omdat de omgevingstemperatuur neutraal was en de vogels slechts 15 minuten per dag vlogen.